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Managing hedgerows for nocturnal wildlife: do bats and their insect prey benefit from targeted agri-environment schemes?

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Abstract

1. Mitigating the detrimental impacts of intensive farming on biodiversity requires the implementation of cost-effective conservation actions. Targeted agri-environment-schemes (AESs) to enhance populations of threatened species inhabiting farmland have been proposed for this purpose, yet their effectiveness for nocturnal wildlife remains unknown.

2. We assessed whether hedgerow management prescribed by targeted AESs to improve habitat conditions for the greater horseshoe bat (*Rhinolophus ferrumequinum*) in England may positively influence the species, the entire bat assemblage and the insect prey of bats. We specifically investigated the responses of bats (occurrence, activity, and species richness) and insects (biomass, abundance, and diversity) to time since last trimming (from 1 up to 10 years). We explored the mechanisms underlying the effects of AES via changes in trimming regime on bats. Moreover, we investigated the effects of landscape context on bats as we expected that highly mobile species would benefit further from landscape-scale management.

3. Bat species richness significantly increased with time since last trimming. Three bat taxa of major conservation concern in Western Europe substantially benefited from the targeted prescription, namely *R. ferrumequinum*, *R. hipposideros* and *Plecotus* spp. Insect-family richness and dipteran abundance were also significantly greater at hedgerows that were untrimmed for at least three years. The activity of more common bat species (i.e. pipistrelle bats) was not influenced by time since last trimming.

4. Changes in trimming regime strongly affected hedgerow height which directly and indirectly (by increasing prey abundance) influenced bat occurrence, activity and species richness along hedgerows.
5. The activity of highly mobile bat species was mainly associated with a range of landscape attributes. The amount of semi-natural grassland within 0.5 km of the sampling sites positively influenced *R. ferrumequinum* while the presence of urban areas negatively affected light-sensitive bat species.
6. *Synthesis and applications.* The implementation of targeted agri-environment-schemes can include effective measures to enhance bats and their insect prey in farmland. Although we highlight the success of current prescriptions on hedgerow management, we suggest that their effectiveness can easily be optimized by encouraging farmers to keep hedgerows untrimmed for longer periods (>3 up to 10 years). We also highlight that a multi-scale management approach is required to successfully promote bats in farmland.

Keywords

Acoustic sampling, Agri-environment schemes, Arthropod, Chiroptera, Farmland, Higher Level Stewardship, Landscape attributes, Multi-scale management.

1. Introduction

Over the past 60 years, agricultural expansion and intensification have contributed substantially to biodiversity loss in European farmlands (Robinson & Sutherland 2002; Stoate *et al.* 2009). To address this issue, Agri-Environment Schemes (AESs) have been promoted by the European Union and have rapidly become the most expensive conservation programme implemented in Europe (Batáry *et al.* 2015). This voluntary incentive-based system provides financial support to farmers that adopt environmentally sustainable land management. However, AESs have met with mixed success despite their high cost (Kleijn *et al.* 2006). A number of different factors have been posed to explain this pattern (Kleijn *et al.* 2011) including landscape-moderated effectiveness of

AESs (Concepción, Diaz & Baquero 2008), and the degree of farmers' involvement in the process (McCracken *et al.* 2015).

A lack of well-designed target prescriptions could also have contributed to the limited success of AESs. By tailoring specific management options to meet the requirements of species of interest in priority areas, targeted AESs have proved to be very effective in promoting farmland biodiversity, including that of insects (e.g., Wood *et al.* 2015) and birds (e.g., Bright *et al.* 2015). However, criticisms include that targeted AESs are expensive and therefore not applicable at broad spatial scales, and that their positive impacts are mostly restricted to a small number of priority species even though there is now evidence that non-targeted species also benefit from these schemes (MacDonald *et al.* 2012b; MacDonald *et al.* 2012c; Wilkinson, Wilson & Anderson 2012; Helden *et al.* 2015). Many targeted schemes crucially lack monitoring that prevents an assessment of their outcomes, and this is especially true for those targeting nocturnal endangered species such as bats (Park 2015). Further evidence is therefore urgently needed as these schemes may have wider positive impacts on biodiversity than originally expected.

In western Europe, many insectivorous bats suffered severe population declines during the late 20th century (Stebbing 1988), partly due to the loss of foraging and commuting habitats in farmland (e.g., removal of hedgerows) and declines in insect populations caused by the increasing use and efficiency of pesticides. Given that bats are now protected within the European Union and considered to play important roles as bioindicators (Jones *et al.* 2009) and in pest suppression in agricultural ecosystems (Russo, Bosso & Ancillotto 2018), it is crucial to mitigate these negative impacts that directly arise from agricultural intensification (Park 2015). The restoration, conservation, and management of key habitat features in farmland to enhance bat populations have generally been implemented through AESs, yet these prescriptions (excluding organic farming; see Wickramasinghe *et al.* 2003) have failed to achieve their objectives (Taylor & Morecroft 2009; Fuentes-Montemayor, Goulson & Park 2011; Angell *et al.* 2019, MacDonald *et al.* 2019).

In England, targeted agri-environment schemes have been employed to improve conditions for the greater horseshoe bat (*Rhinolophus ferrumequinum*), a threatened bat species that is strongly associated with farmland (Duvergé & Jones 2003; Froidevaux *et al.* 2017). Thus, since 1991 tailored land management options have been designed to enhance *R. ferrumequinum* populations. Amongst these, the management of hedgerows seems to be the most important as it may benefit not only *R. ferrumequinum* (Duvergé & Jones 2003) but also (i) other bat species that depend on these linear features to commute and forage (Walsh & Harris 1996); and (ii) bats' insect prey (Maudsley 2000). Nevertheless, despite some recommendations for improving hedgerow management for bats (Boughey *et al.* 2011; Lacoëuilhe *et al.* 2016, 2018), the effectiveness of this targeted prescription in improving habitats for *R. ferrumequinum* and other bat species has not yet been assessed empirically.

The aim of the study was to test the hypothesis that bats and their insect prey may benefit from targeted AESs using the prescriptions on hedgerow management promoted by the Higher Level Stewardship (HLS; contract of 10 years established between 2005-2014; see Appendix S1 in Supporting Information) as a case study. Our first objective was to assess the effect of trimming regime (i.e., time since last trimming) on *R. ferrumequinum* and other bat species by investigating the main HLS recommendation on hedgerow management, namely trimming hedgerows no more than one year in three. Given that *R. ferrumequinum* (Duvergé & Jones 2003) and other short- and mid-range echolocators may favour tall and structurally complex hedgerows (Wickramasinghe *et al.* 2003; Boughey *et al.* 2011; Lacoëuilhe *et al.* 2016), we predicted that most species of bats would benefit from sympathetic trimming management through habitat modifications. We also investigated the responses of nocturnal insects to trimming to determine whether the HLS prescription improves bat foraging opportunities. Our second objective was to unravel the mechanisms by which some bat species may benefit from the implementation of HLS hedgerow prescriptions through changes in trimming regime. Finally, our third objective was to investigate whether the effect of HLS prescriptions on bat activity and species richness along hedgerows could be mediated by landscape attributes (e.g., density of linear features, amount of semi-natural grasslands and broadleaf woodlands) and the presence of grazing in adjacent fields. Because of their mobility and hence their ability to move easily over the wider landscape, we hypothesised that landscape characteristics would

have a strong influence on highly mobile bat species (Fuentes-Montemayor *et al.* 2017). We also predicted that the presence of grazing in fields surrounding the hedgerows would benefit *R. ferrumequinum* (Duvergé & Jones 2003) and other bat species (Ancillotto *et al.* 2017) by increasing prey availability.

2. Materials and methods

2.1. Study area and sampling design

The study was conducted during summer 2016 (from early June to late August) in five counties (Gloucestershire, Somerset, Wiltshire, Devon, Cornwall) in south-west England. We selected 20 pastoral and mixed farms that were under Higher Level Stewardship (HLS) agreements during the period 2005-2016 (see Fig. S1). As bat occurrence and activity may be related to distance to the nearest roost, farms were located at least 750 m and 500 m away from known maternity roosts of *Rhinolophus ferrumequinum* and *R. hipposideros*, respectively (see Table S1 for more details), which correspond to one quarter of their typical maximum foraging distance (Collins 2016). Roosts of *Rhinolophus* spp. are relatively well known and mapped out in the UK. It was not possible, however, to control distance from other bat colonies as the exact location of their roosts were unknown. Nevertheless, when testing responses of *Rhinolophus* species to the distance to the nearest roost, we found that the probability of recording of *R. ferrumequinum* still significantly decreases with increasing distances from the nearest known roost (GLMM; est. \pm SE = -0.13 ± 0.05 , $Z = -2.51$; $P = 0.012$).

Within each farm, we chose one or two hedgerows that were targeted by the prescription “management of hedgerows of very high environmental value” (hereafter referred to as HLS hedgerows). This particular HLS option mentions *Rhinolophus ferrumequinum* as a target species (Natural England 2013). We then matched each HLS hedgerow with one or several hedgerows that were conventionally managed (i.e., trimmed once every one or two calendar years) within the same farm (hereafter referred to as CM hedgerows). We used the land type surrounding the hedgerow (grassland, mixed and arable), hedgerow length (≥ 100 m), terrain slope (visual observation: flat vs.

sloping), as well as the distance to the nearest broadleaf woodland (mean \pm SD; HLS hedgerows: 305 m \pm 184; CM hedgerows: 356 m \pm 225) as main criteria during the matching process. The sampling sites were located at the midpoint of the hedgerows and were situated (i) ≥ 50 m away from other hedgerows and woodland patches; and (ii) ≥ 200 m from each other. In total, 64 hedgerows were selected comprising 30 HLS hedgerows and 34 CM hedgerows.

2.2. Hedgerow characteristics

We conducted field measurements to characterise the hedgerow environment, structure and composition. We defined a hedgerow as a linear feature mainly composed of woody plants that forms part of a management unit with a minimum height of 0.5 m (Baudry, Bunce & Burel 2000). Tree lines were therefore included within our definition. Along each hedgerow, we established a standardized 21 m line transect with its centre located at the sampling site. The transect length chosen was sufficient to capture both structural and compositional variation. The transect was then divided in 14 equal sections of 1.5 m. Within each section, we identified the different species of shrubs and trees. We took 15 measures of hedgerow height (one per section boundary) using a laser distance meter (Tacklife LDM03; accuracy: 2 mm; Shenzhen Temie Technology Co., Shenzhen, China), and one measure of hedgerow width as the latter was fairly constant along the transect. We noted the presence of grazing (sheep or cattle) in the fields surrounding the hedgerow to consider its potential effect on bat activity (Duvergé & Jones 2003; Ancillotto *et al.* 2017). Finally, the farmers provided us information on trimming regime (i.e., time since last top mechanical trimming). We classified this information into three categories, namely:

- 1: hedgerows trimmed during the winter prior to sampling (N=28 including 4 HLS and 24 CM hedgerows);
- 2: hedgerows trimmed two winters prior to sampling (N=17 including 7 HLS and 10 CM hedgerows);

- ≥ 3 : hedgerows not trimmed at least three consecutive winters (N=19 with HLS hedgerows only).

Note that side trimming could have sometimes occurred in hedgerows not top trimmed for >4 consecutive winters.

2.3. Bat echolocation call recording and identification

We sampled bats acoustically along hedgerows using Song Meter SM2BAT recorders (sampling rate: 384 kHz) connected to SMX-U1 omnidirectional ultrasonic microphones (Wildlife Acoustics, Concord, USA) mounted 2 m above ground. Recording was triggered automatically when sounds in the frequency range 12-192 kHz and ≥ 12 dB above background noise were detected, and continued for 15 sec. Hedgerows that were located within the same farm (i.e. matched HLS and CM hedgerows; range: 2-4) were sampled simultaneously during one full night, from 30 min before sunset to 30 min after sunrise. Only one farm was surveyed per night. Sampling took place only during dry, warm (minimum temperature at night > 7 °C) and calm (wind speed < 30 km/h) nights. We monitored temperature at night every 15 minutes using a data logger (RC-5; accuracy: 0.5 °C; Elitech, London, UK).

We manually identified each bat pass (i.e., series of minimum two echolocation calls with inter-pulse intervals < 1 sec) present within each 15 sec recording to the lowest taxonomic level (see Appendix S2) using Batsound 4.1.4. (Pettersson Electronic, Sweden). Identification criteria were based on call characteristics (e.g., frequency of maximum energy, end frequency, and duration, etc.). For each taxon, we quantified bat activity as a proxy of abundance by counting the number of bat passes recorded per night. Occurrence data were also considered for taxa encountered in less than two-thirds of the sites. Species richness was calculated considering species groups (*Plecotus* spp., *Myotis* spp. and *Nyctalus/Eptesicus* spp.) as single taxa. Due to the very low occurrence of *P. nathusii*, this species was disregarded for species-specific analysis.

2.4. Insect sampling

Insects were collected along hedgerows using a portable heath-type actinic light trap (6 W 12 V actinic bulb). Each hedgerow was sampled once, from 30 min before to 4 h after sunset. To avoid any interference between the light trap and the bat detector that may significantly bias the acoustic outcomes (Froidevaux, Fialas & Jones 2018), insects were surveyed on the night after the bat sampling, weather permitting (i.e., similar weather conditions to the bat sampling). Insects trapped were euthanised using a cotton wool ball soaked in ethyl acetate left in the trap for ≥ 10 h and were then placed in a -18 °C freezer until identification. We identified all insects to at least family level (see Appendix S3 for references used) with the exception of aphids that were classed within the Aphidoidea superfamily. After identification, insects were oven-dried at 60 °C for 2-3 days and the dry weight was measured using a 5-digit electronic balance (ALT 100-5AM; accuracy: 0.01 mg; KERN & Sohn GmbH, Balingen, Germany). Finally, we calculated the insect biomass, total insect abundance, dipteran and moth abundance (the two most abundant orders), and insect family richness at each site. Data (except moth abundance) from four hedgerows (one farm) were omitted due to equipment failure.

2.4. Landscape analysis

We created three buffers (0.5, 1.5, and 3.0 km radii) around each of the 64 hedgerows using ArcGIS Desktop v10 (ESRI, Redlands, California, USA). While the larger spatial scales represent the core sustenance zone of many bats present in the study area (Collins 2016), the smallest one allows us to describe the farm environment. We reclassified the Land Cover Map 2015 supplied by the Centre of Ecology and Hydrology (Rowland *et al.* 2017) into 10 categories (see Table S2) and extracted within each buffer the proportion of urban areas, arable lands, improved grasslands, semi-natural grasslands, and broadleaf woodlands. To take into account important linear elements for bats (Walsh & Harris 1996; Verboom & Huitema 1997), we also calculated the density of rivers (OS open Rivers, Ordnance Survey), the density of hedgerows using data from models on “woody linear features” developed by Scholefield *et al.* (2016a,b), and the density of hedgerows using our own dataset (hedgerows mapped based on imageries from Google Earth 2016 following Boughey *et al.* 2011).

Finally, as bats may use hedgerows as commuting routes between woodland patches (Davies & Pullin 2007), we measured the distance to the nearest broadleaf woodland via hedgerows with the ArcGIS Network Analyst extension.

2.5. Statistical analysis

The analyses were conducted in three steps corresponding to the three objectives of the study. We first evaluated the direct effect of trimming regime on hedgerow structure and composition, bats and insects. We then employed a mechanistic approach in a separate analysis to understand how HLS prescription may enhance bat activity and species richness through changes in trimming regime. We finally investigated whether landscape attributes and the presence of grazing could mask the effect of trimming regime on bats by including these variables in models developed in step one. Statistical analyses were conducted using R 3.4.1 (R Development Core Team 2017).

2.5.1. Step one: effect of time since last trimming

We first assessed the effects of trimming regime on (i) hedgerow structure (width, mean and standard deviation of height) and composition (woody plant species richness); (ii) bat species occurrence, activity, and species richness; and (iii) total insect biomass and abundance, dipteran abundance, moth abundance, and insect family richness, by fitting a series of (generalized) linear mixed-effects models (GLMMs & LMMS; “lme4” package; Bates *et al.* 2015). Time since last trimming (categorical variable; see section 2.2) was included as fixed effect while farm nested within county were considered as random effects to account for the hierarchical clustering of sample locations and because AES outcomes may greatly vary between farmers (McCracken *et al.* 2015). For models on bats and insects, the inclusion of temperature at night (see Appendix S4) and Julian day as covariates were assessed using an information-theoretic approach based on the second order Akaike information criterion (AIC_c ; Burnham & Anderson 2002): if the presence of covariates did not lower AIC_c (i.e. $\Delta AIC_c \geq 2$) compared to models incorporating trimming regime only, they were disregarded from the models. We used the same approach for the inclusion of distance to the nearest maternity roost for the model investigating the response of *R. ferrumequinum* occurrence (see section 2.1).

Depending on the nature of the data, we either used a Gaussian distribution (data were log-transformed when necessary to meet normality assumptions), a binomial distribution (with a logit link function) for presence/absence data, or a Poisson distribution (negative binomial when overdispersion was found) for count data. We performed Tukey's post hoc multiple comparison tests ("multcomp" package; Hothorn, Bretz and Westfall 2008) to assess pairwise differences among trimming regime categories. Model validation was conducted using the "DHARMA" package (Hartig 2017).

Because some HLS hedgerows were not trimmed for 3 to ≥ 10 years prior to sampling (see Fig. S2), we were also interested to investigate the long-term effects of non-trimming on bats and insects. We therefore performed a series of generalized additive mixed models (GAMMs; "mgcv" package; Wood 2017) considering time since last management as a continuous (fixed) variable. GAMMs were only conducted on response variables that showed statistical significance ($P < 0.05$) in the previous analyses when investigating differences between hedgerows that were trimmed at least three years prior to sampling and the most recently trimmed ones. We favoured GAMMs rather than (G)LMMs because we expected non-linear relationships between the response and the independent variables. We used the same model structure as previously described.

2.5.2. Step 2: mechanistic approach

To unravel the mechanisms underlying behind the effect of HLS prescription through trimming regime on bats, we sequentially tested the effects of (i) hedgerow management on time since last trimming; (ii) time since last trimming on hedgerow structure; (iii) hedgerow structure on insects and bats; and (iv) insects on bats. More specifically, we first performed a GLMM to investigate the relationship between time since last trimming (from 1 up to 10 years) and hedgerow management (CM vs. HLS hedgerows). We then conducted a series of GAMMs to determine which hedgerow structural or compositional variable had the strongest association with time since last trimming. Mean hedgerow height was retained in the subsequent analyses since its relationship with time since last trimming had the greatest pseudo- R^2 value. We assessed insect responses to hedgerow height using GAMMs as non-linearity was expected. We only performed models on dipteran abundance and insect family richness since previous analyses demonstrated significant effects of trimming regime on these

variables. We finally disentangled the direct and indirect effects of hedgerow structure on bats using mean hedgerow height, dipteran abundance, and insect family richness as explanatory variables in GAMMs. We only considered the responses of three taxa (*R. ferrumequinum*, *R. hipposideros*, *Plecotus* spp.) as well as bat species richness because of their strong relationship found with trimming regime. Since dipteran abundance and insect family richness were highly correlated ($r > 0.7$), the latter was excluded from the models. Model structure and inclusion process of covariates (e.g. temperature at night) were identical to step one.

2.5.3. Step 3: local and landscape effects

To disentangle the effects of landscape characteristics and grazing alongside trimming regime on bats, we conducted a series of (G)LMMs. We considered as fixed effects (i) the interaction between the two categorical variables “time since last trimming” and “presence/absence of grazing” (unbalanced design, see Fig. S3); and (ii) the following continuous variables: Julian day, temperature at night, and landscape attributes (see section 2.4). We chose the same model structure and validation process as previous (G)LMMs developed in step one. To enable comparisons of effect sizes between variables, all continuous variables were standardized prior to their inclusion in the models. To avoid multicollinearity among predictors, we proceeded in two steps. First, we tested independently the relationships between the response variables and each landscape feature using a series of (G)LMMs. For each landscape variable, only the most relevant spatial scale (i.e., the scale in which the variable had the largest coefficient) was selected and included in the final models. Second, we calculated the variance inflation factor (VIF) for each final model; variables with the largest VIF values (i.e., variables highly related with others) were successively removed until all variables had VIF values < 3 (Zuur, Ieno & Elphick 2010). We performed model selection using the *dredge* function (“MuMIn” package; Barton 2016) that allows generating all possible models (see Appendix S5 for further details). We then applied an information-theoretic approach using AIC_c to select the most parsimonious ones (Burnham & Anderson 2002). When models were considered equivalent ($\Delta AIC_c < 2$), we chose the model with the fewest predictors.

3. Results

We recorded 14,509 bat passes along 64 hedgerows in 20 farms located across south-west England (Tables 1 and S3). The bat assemblage was dominated by *P. pipistrellus* with 8,667 bat passes (60% of the total bat activity), followed by *Nyctalus/Eptesicus* spp. (11%), *Myotis* spp. (11%), and *P. pygmaeus* (10%). Most of the bat passes from *R. ferrumequinum*, *B. barbastellus*, *Nyctalus/Eptesicus* spp. and *P. pygmaeus* were recorded within three hours after sunset while the activity of other taxa was relatively more constant through the night (see Fig. S4). In total 8,044 insects (biomass: 69.6 g) were trapped along 60 of the 64 hedgerows sampled. All individuals were classified within 120 families and one superfamily (Table S4). Diptera and Lepidoptera were by far the most abundant insect orders at all sampling sites with a total of 3,944 (49%) and 2,559 (32%) individuals, respectively. Hedgerows were mainly composed of blackthorn (*Prunus spinosa*; dominant species in 26% of the 896 × 1.5 m sections), hawthorn (*Crataegus* spp.; 19%), and hazel (*Corylus avellana*; 15%).

3.1. Effects of trimming regime on hedgerow characteristics, bats and insects

As expected, (G)LMMs indicated that structural (width, mean and standard deviation of height) and compositional (woody plant species richness) complexity of hedgerows significantly increased with time since last trimming (Fig. 1). Regarding bats and insects, significant effects were mainly found between the most recently trimmed hedgerows and those that were trimmed at least three years prior to sampling. The latter harboured greater bat species richness, insect family richness and dipteran abundance than the former (Fig. 1). The effect of trimming regime on bats was, however, taxon-specific. While the activity of *Myotis* spp., *P. pipistrellus*, *P. pygmaeus* and *Nyctalus/Eptesicus* spp. was not significantly influenced by the trimming regime, *R. ferrumequinum* and *Plecotus* spp. were significantly more active along hedgerows that were trimmed at least three years prior to sampling (Fig. 1). For instance, our model suggests that *R. ferrumequinum* activity was almost four-fold higher along hedgerows that were not trimmed for at least three consecutive years than hedgerows that were trimmed one winter prior to sampling. We found a similar pattern regarding the

occurrence of *R. ferrumequinum*, *R. hipposideros* and *Plecotus* spp.: our models suggested that we were less likely to record these taxa along recently trimmed hedgerows compared with other hedgerow types. Hedgerows that remained untrimmed for at least three years seemed to positively influence the occurrence of *B. barbastellus* with both lower and higher confidence intervals of the estimates being positive. Nevertheless, only marginal significance was found (≥ 3 vs. 1: $P = 0.096$; ≥ 3 vs. 2: $P = 0.058$).

3.2. Long-term effects of non-trimming

Bat species richness (GAMM; $edf = 1.81$, $F = 10.18$, $P < 0.001$), insect family richness (GAMM; $edf = 1.00$, $F = 5.26$, $P = 0.030$) as well as *R. ferrumequinum* (GAMM; $edf = 1.00$, $F = 6.21$, $P = 0.015$) and *Plecotus* spp. (GAMM; $edf = 1.00$, $F = 17.31$, $P < 0.001$) activity were positively related to time since last trimming (Fig. 2). Likewise, the probability of recording *R. ferrumequinum* (GAMM; $edf = 1.00$, $F = 5.50$, $P = 0.022$) and *Plecotus* spp. (GAMM; $edf = 1.00$, $F = 8.51$, $P = 0.005$) significantly increased with time since last trimming while the effect was only marginal for *R. hipposideros* occurrence (GAMM; $edf = 1.80$, $F = 2.07$, $P = 0.083$). A bell-shaped curve was detected when investigating the long-term effect of trimming regime on dipteran abundance (GAMM; $edf = 2.35$, $F = 7.14$, $P = 0.001$; Fig. 2), even though confidence intervals are large.

3.3. Understanding the mechanisms

Changes in trimming regime was the main HLS prescription on hedgerow management and HLS hedgerows were therefore trimmed less often than CM ones (GLMM; est. \pm SE = 1.40 ± 0.17 , $Z = 8.24$, $P < 0.001$; Fig. 3). Among the four compositional/structural hedgerow variables, changes in trimming regime had the strongest effect on mean hedgerow height (GAMM; $edf = 2.78$, $F = 79.92$, $P < 0.001$; Figs. 3 and S5). Both insect family richness (GAMM; $edf = 1.00$, $F = 4.53$, $P = 0.038$) and dipteran abundance (GAMM; $edf = 1.00$, $F = 9.84$, $P = 0.003$) responded positively to increases in hedgerow height (Fig. 3). When assessing the direct and indirect effect of hedgerow structure on bats, we found that *Plecotus* spp. occurrence (GAMM; $edf = 1.00$, $F = 5.07$, $P = 0.028$) and activity (GAMM; $edf = 1.00$, $F = 7.37$, $P = 0.009$) were positively and directly influenced by hedgerow

height while the two *Rhinolophus* species responded to the increase of dipteran abundance (GAMMs; *R. ferrumequinum* occurrence: $edf = 1.00$, $F = 4.30$, $P = 0.043$; *R. hipposideros* activity: $edf = 1.00$, $F = 8.85$, $P = 0.004$) which was induced by the increase of hedgerow height (Fig. 3). The probability of recording *R. hipposideros* as well as *R. ferrumequinum* activity were not influenced by any of the variables evaluated.

3.4. Influence of local and landscape factors on bats

The activity and probability of recording *R. ferrumequinum* was enhanced by the proportion of semi-natural grassland at the smallest spatial scale (0.5 km; Fig. 4; $P = 0.050$ and $P = 0.007$, respectively). *Myotis* spp. activity was positively related to the proportion of improved grassland and the proportion of arable land negatively affected the activity of *P. pipistrellus* (Table 2). The density of linear elements had contrasting effects on bats depending on their nature (rivers, hedgerows, or woody linear features) and on the spatial scales considered. For instance, the density of hedgerows had a negative impact on the activity of *P. pygmaeus* and *Nyctalus/Eptesicus* spp. (Table 2). Although sampling took place in farmland-dominated landscapes, the proportion of urban area negatively influenced the activity of *Nyctalus/Eptesicus* spp. ($P = 0.033$), *B. barbastellus* ($P = 0.055$), and *R. hipposideros* ($P = 0.059$), even though the effect was only marginal for the two last species. The probability of recording *B. barbastellus* also significantly decreased with increasing amount of urban area ($P = 0.031$). Even after the inclusion of local and landscape attributes into the models, best model selection showed that the effect of trimming regime remained significant for models on bat species richness, *Plecotus* spp. activity, *R. ferrumequinum* and *R. hipposideros* occurrence (Table 2). However, trimming regime was not retained in the most parsimonious model related to the activity of *R. ferrumequinum* since the proportion of semi-natural grassland at 0.5 km radius scale appeared to be a stronger predictor. No evidence for an effect of sheep or cattle grazing on bats was found.

4. Discussion

The potential value of targeted AESs on bats has received little attention, yet these schemes have proved to be very effective in enhancing populations of other target (Bright *et al.* 2015; Wood *et al.* 2015) and non-target species (MacDonald *et al.* 2012a; MacDonald *et al.* 2012b; Wilkinson, Wilson & Anderson 2012; Helden *et al.* 2015). This study provides empirical evidence that changes in trimming regime implemented through the HLS prescriptions can positively affect several bat species and their insect prey. Our findings also highlight that tailored management targeting one particular threatened species (here *Rhinolophus ferrumequinum*) may benefit other taxa and, therefore, emphasize the success of targeted AESs for promoting biodiversity in farmland. Finally, because wider landscape attributes strongly predict bat occurrence and activity along hedgerows, implementing a multi-scale management approach (i.e., from farm field to landscape) for the conservation of highly mobile taxa in agricultural landscapes is paramount.

4.1. The effects of hedgerow management on bats and their insect prey

The implementation of sympathetic hedgerow management had a positive influence on three bat taxa that are of major conservation concerns in Western Europe, namely *R. ferrumequinum*, *R. hipposideros*, and *Plecotus* spp. A similar trend was also found for *B. barbastellus*, although not significant. Our mechanistic approach demonstrates that while *Plecotus* spp. responded directly to increasing hedgerow height induced by the sympathetic management, the two *Rhinolophus* species responded indirectly through changes in prey availability. Two key mechanisms seem therefore to be involved. First, reducing trimming frequency may improve the quality of hedgerows as corridors. In farmland-dominated landscapes, these short-range echolocator species mainly rely on linear features for commuting from their roost to foraging patches (Limpens & Kapteyn 1991), and untrimmed hedgerows may act as better acoustic landmarks than annually trimmed ones due to their greater height, roughness, and width. Second, the implementation of sympathetic trimming regime may increase foraging opportunities for bats. Tall hedgerows were associated with greater abundance of dipterans and increased diversity of insect families. Furthermore, several studies have emphasized that

reduced trimming frequency enhances moth abundance of specific guilds at both larval (Facey *et al.* 2014; Staley *et al.* 2016) and adult (Froidevaux, Broyles & Jones 2019) stages. Given that moths constitute the main prey items of *R. ferrumequinum* and *Plecotus* spp., and flies are a major food source for *R. hipposideros* and to a smaller extent *R. ferrumequinum* (Vaughan 1997), it is then very likely that these species favour foraging along untrimmed hedgerows due to high prey availability.

Despite the strong affinity of pipistrelle bats for hedgerows (Verboom & Huitema 1997), their activity was not affected by the management conducted. The responses of pipistrelle bats to hedgerow management and characteristics are complex and still unclear as several studies conducted in the same geographical area (Britain) found different patterns. Our findings are in line with those of Fuentes-Montemayor, Goulson & Park (2011) who found no differences when comparing pipistrelle activity between conventionally-managed hedgerows and hedgerows under AES prescription in Scotland. Nevertheless, these results only partly support those of Boughey *et al.* (2011) who highlighted contrasting effects of hedgerow characteristics in England on *P. pygmaeus* and *P. pipistrellus*, with a positive association found between the occurrence of the former with tree density. In Wales, *P. pipistrellus* seems to respond negatively to increases in hedgerow height and width (Angell *et al.* 2019). Further work is needed to better understanding how the most common bat species in Europe are affected by hedgerows as they might play a major role (due to their high abundance) in pest suppression in farmland (Russo, Bosso & Ancillotto 2018).

As expected, there were no differences in *Nyctalus/Eptesicus* spp. activity between the three hedgerow categories. These long-range echolocator species that are adapted for fast and high flight above pasture and forest canopy (Harris & Yalden 2008) are more likely to be affected by a broad-scale management. It is important to point out that none of the bat species recorded was negatively associated with the implementation of sympathetic trimming regime and that, overall, bat species richness was significantly greater along hedgerows trimmed less frequently.

4.2. Landscape attributes influencing bats along hedgerows

Species mobility has been identified as a key trait in determining the relative effects of local and landscape attributes on bats (Fuentes-Montemayor *et al.* 2017). Our findings support this suggestion, as the activity and occurrence of *Plecotus* spp. (i.e., relatively low mobile taxa) was not influenced by any of the landscape variables while the activity of the *Nyctalus/Eptesicus* spp. (i.e., highly mobile group) was mainly driven by a range of landscape attributes. Our results also identified the influence of landscape features on other bats, but at different spatial scales and extents. The proportion of semi-natural grassland was a strong predictor of *R. ferrumequinum* occurrence and activity. While the landscapes were largely dominated by agricultural land, the activity of *R. hipposideros*, *B. barbastellus* and *Nyctalus/Eptesicus* spp. were negatively impacted by urban areas, even when these represented on average <10% of the landscapes (means of 1 and 8% at 0.5 and 1.5 km radius scales, respectively). Given that the two first species are light-averse, the negative relationship found may indicate a strong effect of light pollution arising from urban areas on adjacent habitats (Rowse *et al.* 2016). In contrast, *Nyctalus/Eptesicus* spp. actively forage in lit areas and urban areas may be more attractive for these species than farmland, at least at small spatial scales. In the UK, *Myotis* spp. (except *M. daubentonii*) are mainly associated with woodland habitats for foraging (Harris & Yalden 2008), yet we found a positive relationship between their activity and the amount of improved grassland. This counter intuitive result may suggest that in agricultural landscapes where high quality habitats such as woodlands are unavailable, hedgerows are more intensively used by *Myotis* spp. as they constitute a suitable alternative habitat. This is particularly true for *M. mystacinus* and *M. nattereri* (Harris & Yalden 2008). Similarly, the surprising negative effect found between the density of hedgerows and tree lines and the activity of some bat species may be due to habitat availability. As suggested by Fuentes-Montemayor *et al.* (2013), bats are more likely to concentrate their foraging activities in few habitat patches in landscapes in which the resources are scarce as flying long distances to remote habitats is energetically costly.

4.3. Implications for conservation and recommendations for the design of AESs

Hedgerows play a vital role in conserving biodiversity in farmland (Graham *et al.* 2018) and support multiple ecosystem services (Dainese *et al.* 2017), yet a majority of them are in poor structural conditions due to a lack of appropriate management. Our results suggest that substantially reducing trimming frequency constitutes a key conservation measure to counteract the negative effects of over-trimming on bat species that are subject of major conservation concerns and may, in addition, have wide biodiversity benefits. Given that hedgerows constitute distinctive landscape features in many farmlands worldwide, this measure is of relevance globally and may be easily applied by farmers as it is less labour-intensive and costly in the long term than conventional management. While the less severe trimming regime prescribed by previous and current AESs in England encourages farmers to trim hedgerows only one year in three, our study largely supports the longer-term benefits of non-trimming on bats and their insect prey. Keeping in the farm some hedgerows untrimmed for up to 10 years would enhance bat species richness and insect family diversity. AES prescriptions should therefore offer more incentives to not trim hedgerows for a longer period. We, however, emphasize the necessity to trim hedgerows after a certain lapse of time because unmanaged hedgerows may in the long term be disconnected from each other due to the emergence of large gaps that may negatively affect bats through the loss of habitat connectivity (Pinaud *et al.* 2018). As currently prescribed, avoiding trimming every hedgerows in the same year would therefore be of greatest benefit. Finally, results indicate that site-level management actions should be accompanied by the implementation of landscape-scale conservation actions to successfully conserve bats in agricultural landscapes. These include (i) increasing foraging habitat availability in the landscape through the conservation and restoration of semi-natural habitats (e.g., semi-natural grassland for *R. ferrumequinum*) and the reduction of areas under intensive agriculture (e.g., arable lands); and (ii) limiting and mitigating the impacts of anthropogenic pressures such as light pollution for light-averse bats.

Authors' Contributions

JSPF and GJ co-designed the study, JSPF collected and analysed field data, MB identified the insects, GJ and KLB were involved in study co-ordination, JSPF led the writing of the manuscript, GJ, KLB, and CLH contributed critically to the drafts. All authors gave final approval for publication.

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Data accessibility

Data available via the Dryad Digital Repository <https://doi.org/10.5061/dryad.6970v40> (Froidevaux *et al.* 2019).

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Tables

Table 1. Summary table of bat activity (mean number of bat passes \pm standard deviation, and total number of bat passes) recorded along the three categories of hedgerows that differ in trimming regime (i.e. time since last top mechanical trimming).

Taxa	Time since last trimming (years)			Total
	1 (N = 28)	2 (N = 17)	≥ 3 (N = 19)	
<i>Barbastella barbastellus</i>	0.68 \pm 2.48	3.12 \pm 8.75	6.32 \pm 14.19	192
<i>Myotis</i> spp.	33.68 \pm 59.59	23.47 \pm 74.10	12.32 \pm 19.04	1576
<i>Nyctalus/Eptesicus</i> spp.	18.46 \pm 26.58	19.59 \pm 30.96	38.26 \pm 113.48	1577
<i>Pipistrellus nathusii</i>	1.18 \pm 3.14	0.88 \pm 3.64	0.63 \pm 1.92	60
<i>Pipistrellus pipistrellus</i>	128.14 \pm 177.41	73.53 \pm 120.12	201.53 \pm 356.09	8667
<i>Pipistrellus pipistrellus-nathusii</i> [†]	4.46 \pm 13.48	0.12 \pm 0.49	3.11 \pm 10.27	186
<i>Pipistrellus pipistrellus-pygmaeus</i> [†]	1.82 \pm 4.16	1.41 \pm 3.69	2.74 \pm 5.52	127
<i>Pipistrellus pygmaeus</i>	28.57 \pm 45.76	23.53 \pm 56.68	11.42 \pm 15.81	1417
<i>Plecotus</i> spp.	0.46 \pm 0.96	1.65 \pm 2.03	1.90 \pm 3.20	77
<i>Rhinolophus ferrumequinum</i>	0.54 \pm 0.92	2.53 \pm 7.68	3.26 \pm 6.67	120
<i>Rhinolophus hipposideros</i>	8.14 \pm 13.72	9.94 \pm 16.76	5.95 \pm 8.96	510
Total	6332	2716	5461	14509

[†] *Pipistrellus* species that could not be identified at species level.

Table 2. Results of the most parsimonious (G)LMMs testing the effects of landscape characteristics, grazing, and trimming regime on bats and insects. Marginal R^2 (variance explained by the fixed effects only) of each model as well as the standardized estimates (effect size), standard errors (SE), test statistics (Z value), and P -values of each variable are given. The spatial scale of each landscape attribute is given in brackets. The full description of the most parsimonious models can be found in Table S5.

Response variable	Explanatory variable	Estimate (\pm SE)	Z value	P
<i>R. ferrumequinum</i> occurrence [†] ($R^2 = 0.48$)	Time since last trimming (2) [§]	1.21 (\pm 0.78)	1.55	NS
	Time since last trimming (≥ 3) [§]	2.50 (\pm 0.87)	2.86	*
	% semi-natural grassland (0.5 km)	0.96 (\pm 0.49)	1.96	.
	Distance to the nearest maternity roost	-1.23 (\pm 0.46)	-2.67	**
<i>R. ferrumequinum</i> activity [‡] ($R^2 = 0.47$)	Temperature	0.68 (\pm 0.25)	2.68	**
	% semi-natural grassland (0.5 km)	0.60 (\pm 0.21)	2.90	**
<i>R. hipposideros</i> occurrence [†] ($R^2 = 0.07$)	Time since last trimming (2) [§]	2.62 (\pm 1.15)	2.29	*
	Time since last trimming (≥ 3) [§]	2.96 (\pm 1.13)	2.63	**
<i>R. hipposideros</i> activity [‡] ($R^2 = 0.37$)	% urban (0.5 km)	-0.98 (\pm 0.52)	-1.89	.
<i>B. barbastellus</i> occurrence [†] ($R^2 = 0.60$)	Density of rivers (1.5 km)	1.08 (\pm 0.49)	2.22	*
	% urban (1.5 km)	-2.16 (\pm 1.00)	-2.15	*
<i>B. barbastellus</i> activity [‡] ($R^2 = 0.70$)	Time since last trimming (2) [§]	-0.92 (\pm 0.84)	-1.10	NS
	Time since last trimming (≥ 3) [§]	1.02 (\pm 0.69)	1.48	NS
	Julian day	1.39 (\pm 0.49)	2.83	**
	% urban (1.5 km)	-2.00 (\pm 1.03)	-1.94	.
<i>Plecotus</i> spp. occurrence [†] ($R^2 = 0.23$)	Time since last trimming (2) [§]	1.86 (\pm 0.92)	2.03	*
	Time since last trimming (≥ 3) [§]	2.68 (\pm 1.00)	2.68	**
<i>Plecotus</i> spp. activity [‡] ($R^2 = 0.38$)	Time since last trimming (2) [§]	0.46 (\pm 0.51)	0.91	NS
	Time since last trimming (≥ 3) [§]	1.19 (\pm 0.44)	2.71	**
	Julian day	0.64 (\pm 0.23)	2.72	**
<i>Myotis</i> spp. activity [‡] ($R^2 = 0.33$)	% improved grassland (3.0 km)	0.88 (\pm 0.32)	2.74	**
<i>P. pipistrellus</i> activity [‡] ($R^2 = 0.46$)	% arable (3.0 km)	-0.64 (\pm 0.24)	-2.67	**
	% semi-natural grassland (3.0 km)	-0.48 (\pm 0.22)	-2.21	*
<i>P. pygmaeus</i> activity [‡] ($R^2 = 0.35$)	Density of hedgerows (1.5 km)	-1.08 (\pm 0.42)	-2.59	**
	Density of woody linear features (0.5 km)	0.86 (\pm 0.26)	3.35	***
<i>Nyctalus/Eptesicus</i> spp. activity [‡] ($R^2 = 0.41$)	Density of hedgerows (3.0 km)	-1.09 (\pm 0.36)	-3.06	**
	Density of rivers (3.0 km)	0.86 (\pm 0.34)	2.51	*
	Density of woody linear features (0.5 km)	-0.54 (\pm 0.17)	-3.12	**
	% urban (0.5 km)	-0.64 (\pm 0.30)	-2.14	*
Species richness [¶] ($R^2 = 0.21$)	Time since last trimming (2) [§]	1.00 (\pm 0.43)	2.32	*
	Time since last trimming (3) [§]	1.91 (\pm 0.35)	5.44	***

[†] GLMMs with a binomial distribution; [‡] GLMMs with a negative binomial distribution; [¶] LMMs (Gaussian distribution)

[§] Time since last trimming (1) was the reference category. No post hoc test was applied.

NS: $P \geq 0.10$; . $P < 0.10$; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

Figures

Figure 1. Effects of trimming regime (time since last trimming) on (i) hedgerow structural and compositional characteristics; (ii) bat occurrence, activity, and species richness; and (iii) insect biomass, abundance, and family richness. Estimates and associated 95% confidence interval arising from the Tukey's post hoc test that followed (G)LMMs are shown with symbols (square: hedgerow categories 2 vs. 1; circle: hedgerow categories ≥ 3 vs. 1; triangle: hedgerow categories ≥ 3 vs. 2) and black solid lines, respectively. Values on the right side of the dotted lines suggest a positive effect.

Rfer: *Rhinolophus ferrumequinum*, *Rhip*: *R. hipposideros*, *Bbar*: *Barbastella barbastellus*, *Plec*: *Plecotus* spp., *Myo*: *Myotis* spp., *Ppip*: *Pipistrellus pipistrellus*, *Ppyg*: *P. pygmaeus*, *Nyc/Ept*: *Nyctalus/Eptesicus* spp. · $P < 0.10$; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

Figure 2. Predicted responses of bats and insects in relation to time since last trimming. Model predictions from GAMMs and associated 95% confidence intervals are represented by the black solid lines and grey shaded areas, respectively. Raw data are represented with open circles with size being proportional to the number of overlapping observations in graphs on bat occurrence.

^a For sake of clarity in graphs on *R. ferrumequinum* and *Plecotus* spp. activity, some observations are not displayed (three and one, respectively).

Figure 3. Left panel: summary diagram of the mechanisms underlying the effect of HLS prescription via trimming regime on bats. * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$. Right panel: model predictions and associated 95% confidence intervals of the relationships displayed on the diagram (corresponding letters). Open circles: conventionally-managed hedgerows; Filled black circles: hedgerows under HLS prescription (i.e., with sympathetic trimming regime).

Figure 4. Predicted responses of *R. ferrumequinum* in relation to the amount of semi-natural grassland at 0.5 km radius scale. Model predictions from GLMMs are represented by the black solid lines with 95% confidence intervals indicated in grey. Open circles: hedgerow category 1; filled grey circles: hedgerow category 2; black filled circles: hedgerow category ≥ 3 .

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Description of the targeted agri-environment prescription “maintenance of hedges of very high environmental value”.

Appendix S2. Bat echolocation call identification.

Appendix S3. List of references used for the insect identification.

Appendix S4. PCA on temperature data.

Appendix S5. Description of the model selection process.

Table S1. Results of LMMs built to test whether distances to the nearest *Rhinolophus ferrumequinum* and *R. hipposideros* maternity roosts differ between CM and HLS hedgerows.

Table S2. Description of the reclassified Land Cover Map 2015 classes.

Table S3. Summary table of bat activity (mean number of bat passes) recorded in each farm.

Table S4. Summary table of the number of insects collected along hedgerows.

Table S5. Description of the most parsimonious (G)LMMs relating the effects of local and landscape variables on bat occurrence, activity, and species richness.

Figure S1. Locations of the 20 farms sampled across south-west England.

Figure S2. Histogram of “time since last trimming” distribution.

Figure S3. Mosaic plot illustrating the proportion of hedgerow surrounded by grazing land in at least one of the adjacent fields in relation to trimming regime categories.

Figure S4. Nightly temporal patterns of bat activity.

Figure S5. Responses of mean hedgerow height, standard deviation of height, hedgerow width, and woody plant species richness in relation to time since last trimming (from 1 up to 10 years).





